

## Helminth Parasites of Four Species of Aquatic Snakes from Two Habitats in Southeastern Louisiana

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**ABSTRACT:** A total of 202 specimens of water snakes (*Nerodia* spp.) and 17 cottonmouths (*Agkistrodon piscivorus*) were collected from 2 localities in southeastern Louisiana between March and December 1989, and examined for helminths. Six species of trematodes, 4 cestodes, 9 nematodes, and 2 acanthocephalans were recovered from these snakes. At the Head of Island locality, *Dasymetra villicaeca* and *Proteocephalus variabilis* had the highest prevalence and abundance in *Nerodia cyclopion*; *D. villicaeca*, *Styphlodora magna*, and *Terranova caballeroi* displayed the broadest host specificity, infecting all snakes from Head of Island. Species richness and mean number of individuals were highest in *N. cyclopion* and *A. piscivorus*, but diversity was highest in *N. fasciata*. *Proteocephalus perspicua* and *P. variabilis* were most prevalent and abundant in *N. cyclopion* at the Spanish Lake locality; *Ochetosoma aniarum* and *Kalicephalus rectiphilus* displayed broadest host specificity, infecting all snakes from Spanish Lake. Species richness and mean number of individuals were highest in *N. cyclopion*, while diversity was highest in *A. piscivorus*. In general, higher prevalence, abundance, species richness, and mean number of individuals occurred in snakes from Head of Island. The helminth fauna of *Nerodia* spp. were most similar, reflecting close phylogenetic affinities and broad overlap in diet. In contrast, the helminth fauna of the viperid, *A. piscivorus*, contained 5 helminths that were restricted to this snake. We propose that host diet, habitat differences, and phylogeny are the most important determinants of the helminth fauna of aquatic snakes.

**KEY WORDS:** Trematoda, Cestoda, Nematoda, Acanthocephala, helminths, survey, *Nerodia* spp., *Agkistrodon piscivorus*, snakes, Louisiana.

The helminth communities of fishes, birds, and mammals have been well studied and many theoretical predictions of parasite community organization have originated from these studies. However, the helminth communities of amphibians and reptiles have not been as well characterized as those of other vertebrates. Recently, Aho (1990) summarized what is known of the organization of helminth communities in these hosts. He concluded that their helminth communities are, in general, "highly variable, depauperate, and have traits characteristic of non-interactive community structure." Phylogenetic differences among hosts, as well as local environmental conditions, were shown to be important determinants of helminth community composition.

Several excellent studies of the helminth communities of frogs, salamanders, and turtles have been published (Esch et al., 1979a, b; Goater et al., 1987; Muzzall, 1991a, b), but little quantitative data exist for snake helminth communities. Most studies of the parasites of aquatic snakes have emphasized the taxonomy of certain groups

of parasites. However, several surveys have been concerned with the ecological relationships between helminth parasites and their snake hosts. Collins (1969) conducted a comparative study of the helminths of water snakes (*Nerodia* spp.) and the cottonmouth (*Agkistrodon piscivorus*) in North Carolina, and Dettlerline et al. (1984) compared the helminths of *A. piscivorus* and 3 species of *Nerodia* in Alabama. Studies of the overwintering of helminths in *Thamnophis sirtalis* (Rau and Gordon, 1978), host specificity of snake helminths (Rau and Gordon, 1980), and other general surveys have been published (Anderson, 1935; Gibson and Rabalais, 1973; Camp, 1980). The taxonomy and life histories of snake trematodes in Louisiana have been well studied (Byrd, 1935; Bennett, 1935, 1938; Rabalais, 1967, 1968, 1969a, b; Rabalais and Henson, 1968), but no complete surveys of the helminth fauna of Louisiana snakes have been published. In Louisiana, the cottonmouth and water snakes co-occur in many habitats and prey upon similar food items (Mushinsky, 1987). Because of these ecological similarities, this system presented an opportunity to compare the helminth faunas among these sympatric hosts. The objectives of this study were: 1) to determine the prevalence and abundance of helminths in aquatic snakes, 2) to compare

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the helminth faunas of *Nerodia* spp. and *A. piscivorus*, and 3) to compare the helminth community structures of aquatic snakes from 2 different localities.

### Materials and Methods

Snakes were collected from 2 freshwater localities in southeastern Louisiana. The Head of Island (HOI) study area was located near Head of Island, Louisiana, in Livingston Parish. The HOI locality consisted primarily of cypress-tupelo gum swamp, with some bottomland hardwood forest. The main waterway from which snakes were collected was the Petite Amite River, a natural meandering river with many fallen trees, stumps, and logs. At HOI, the swamp canopy closely follows the courses of the Petite Amite; few large open water areas are present.

The Spanish Lake (SL) study area was a swamp-bayou system located in Ascension Parish, Louisiana. This area has been described by Hebrard and Mushinsky (1978), but in general was characterized as a cypress-tupelo gum swamp with some areas of bottomland forest present. The major waterways are Spanish Lake, Alligator Bayou, Bayou Braud, and Bayou Paul. The presence of Spanish Lake, a large water body, differentiates the SL study area from HOI in that large open expanses of water are present. We observed a greater degree of fluctuation of water levels at SL than at HOI.

A total of 219 snakes including 108 green water snakes, *Nerodia cyclopion* (Dumeril, Bibron, and Dumeril, 1854), 59 broad-banded water snakes, *N. fasciata* (Linnaeus, 1766), 35 diamond-backed water snakes, *N. rhombifera* (Hallowell, 1852), and 17 cottonmouths, *Agkistrodon piscivorus* (Lacepede, 1789) were collected. Snakes were captured by hand, with Pillstrom tongs, or by shooting between March and December 1989. Most snakes were maintained in a refrigerator at 7°C to minimize parasite loss and were usually necropsied within 7 days of capture. Snakes were killed with MS-222 (ethyl m-aminobenzoate methane sulfonic acid) injected intracardially. Snakes that were shot were examined immediately or frozen at -18°C for later examination. Snakes that were frozen included 81 *N. cyclopion*; no other snake species were frozen before necropsy. Taxonomy of snake hosts follows Dundee and Rossman (1989).

The gastrointestinal tract, spleen, liver, gall bladder, heart, lungs, trachea, kidneys, reproductive tract, and oral cavity were examined for helminths. Larval parasites occurred commonly and in large numbers, but were not included in this study. Trematodes were fixed using Berland's solution (1 part formalin : 9 parts acetic acid) and placed in AFA. Cestodes were killed with hot water (90°C) and fixed in AFA. Nematodes were fixed with Berland's solution and transferred to a solution of 70% ethanol and 5% glycerin. Acanthocephalans were placed in 7°C distilled water for 24 hr, and then fixed in AFA. Trematodes, cestodes, and acanthocephalans were stained with Semichon's carmine. Whole mounts of nematodes were made using glycerin jelly. Voucher specimens of helminths were deposited in the United States National Parasite Collection, Beltsville, Maryland (accession nos. 84845-84861;

85272-85275). Ecological terminology conforms to the definitions of Margolis et al. (1982). Chi-square analysis was used to test for differences in prevalence between sexes. Mann-Whitney *U*-tests were used for 2-sample testing. Species richness is the mean number of helminth species per snake. Helminth species diversity was characterized with the Shannon-Weiner diversity index using common logarithms (Zar, 1984). Percent similarity and Jaccard's coefficients were also used to compare communities. These indices were calculated using Ecological Analysis-PC, Oakleaf Systems, P.O. Box 472, Decorah, Iowa 52101. Original data from all snakes are available from the senior author.

### Results

Body sizes (snout-vent length) of all snakes are presented in Table 1. Twenty-one helminth species (6 Trematoda, 4 Cestoda, 9 Nematoda, and 2 Acanthocephala) were recovered from the 4 snake species examined (Tables 2, 5). There was no significant difference in prevalence regardless of parasite species with respect to host sex for all snake species ( $P > 0.05$ ) from both localities. However, abundances of *Ochetosoma aniarum* and *Dasymetra villicaeca* were significantly higher in females of *N. cyclopion* at HOI ( $P < 0.05$ ). No significant difference in species richness ( $P > 0.05$ ) was found between sexes for all snake species from both localities. However, mean number of individual helminths per host was significantly higher in females of *N. cyclopion* at HOI ( $P < 0.01$ ).

Nineteen helminth species infected snakes from the HOI locality (Table 2). Within *Nerodia* spp., highest prevalence and abundance of *Dasymetra villicaeca* and *Pneumatophilus variabilis* occurred in *N. cyclopion*. Prevalence of *Ochetosoma aniarum* was highest in *N. cyclopion*, but abundance was greatest in *N. fasciata*. *Styphlodora magna* infected all species of HOI snakes, but prevalence and abundance was highest in *Agkistrodon piscivorus*. *Ochetosoma laterotrema* was abundant in *A. piscivorus*, but did not occur in other snakes. Similarly, *Proteocephalus agkistrodontis* and *P. marenzelleri* were prevalent (>70%), but their host distribution was limited to *A. piscivorus*. *Proteocephalus perspicua* infected all species of *Nerodia*, with highest prevalence and abundance in *N. cyclopion*. Abundance of *P. variabilis* was highest for all cestodes; however, this helminth only occurred in *N. cyclopion*. *Rhabdias fuscovenosa* was found in all *Nerodia* spp., but *R. eustreptos* was specific to *A. piscivorus*. Another nematode, *Terranova caballeri*, infected all species of snakes from HOI,

Table 1. Body sizes of aquatic snakes from Head of Island and Spanish Lake, Louisiana.

	Nerodia cyclopion		Nerodia fasciata		Nerodia rhombifera		Agkistrodon piscivorus	
	Head of Island	Spanish Lake	Head of Island	Spanish Lake	Head of Island	Spanish Lake	Head of Island	Spanish Lake
N	48	60	30	29	11	24	10	7
Snout-vent length (cm)	60.2 ± 1.2*	63.0 ± 1.5	55.1 ± 1.7	47.8 ± 2.0	81.7 ± 3.6	62.1 ± 4.6	60.5 ± 2.1	60.9 ± 6.8
Range (cm)	44.5-78.5	32.0-81.5	33.7-70.0	28.0-70.0	63.3-100.5	22.0-113.0	53.0-71.5	38.5-84.0

\* Standard error.

but was most abundant in *N. cyclopion* and *A. piscivorus*.

From a community perspective, species richness and mean number of individuals at HOI were highest in *N. cyclopion* and *A. piscivorus*, with a mean of >6 species of helminths and >300 individuals per snake (Table 3). Species richness and mean number of individuals were markedly lower in *N. fasciata* and *N. rhombifera*, but values were similar between these 2 snakes. The Shannon-Weiner species diversity index was highest for the helminth community of *N. fasciata*, while *A. piscivorus* harbored the least diverse helminth community. Jaccard's coefficient and percent similarity indicated that helminth community structure was most similar among *Nerodia* spp. The helminth community of *A. piscivorus* was distinct, reflecting the unique helminths restricted to this snake (Table 4).

Snakes from SL harbored a total of 17 helminth species (Table 5). *Ochetosoma aniarum*, *D. villicaeca*, and *P. variabilis* were most abundant in *N. rhombifera*. *Ochetosoma kansense*, *S. magna*, *Proteocephalus agkistrodontis* and *P. marenzelleri* were only found in *A. piscivorus*. *Proteocephalus perspicua* infected all species of snakes at SL, but highest prevalence and abundance occurred in *N. cyclopion*. *Proteocephalus variabilis* was the most prevalent and abundant helminth at SL, but was specific to *N. cyclopion*. *Kalicephalus rectiphilus* infected all snakes at SL, but was most prevalent and abundant in *A. piscivorus*. *Rhabdias fuscovenosa* infected all species of *Nerodia* at SL; however, *R. eustreptos* was specific to *A. piscivorus*.

Species richness was highest at SL in *N. cyclopion* and *A. piscivorus* (Table 3). Species richness was markedly lower for *N. fasciata* and *N. rhombifera*. Mean number of individuals was highest in *N. cyclopion* and *N. rhombifera*. Values of Shannon-Weiner species diversity were highest for the helminth communities of *A. piscivorus* and *N. fasciata*; *Nerodia cyclopion* had the least diverse helminth community. Analysis with Jaccard's coefficient revealed that helminth community structure of *Nerodia* spp. was most similar (Table 6). In general, the helminth community of *A. piscivorus* exhibited little overlap with *Nerodia* spp. However, analysis of percent similarity indicated that the helminths of *N. rhombifera* and *N. fasciata* were quantitatively most similar (Table 6).

When comparing snakes from HOI and SL, prevalence and abundance of most helminths

Table 2. Prevalence and abundance (mean  $\pm$  SE) of helminths in 4 species of sympatric aquatic snakes from Head of Island, Louisiana.

Parasite species	<i>Nerodia cyclopion</i> N = 48		<i>N. fasciata</i> N = 30		<i>N. rhombifera</i> N = 11		<i>Agkistrodon piscivorus</i> N = 10	
	Prevalence %	Abundance	Prevalence %	Abundance	Prevalence %	Abundance	Prevalence %	Abundance
<b>Trematoda:</b>								
<i>Ochetosoma aniarum</i> (Leidy, 1891)	88	19.1 $\pm$ 6.7	67	22.6 $\pm$ 8.6	73	9.6 $\pm$ 5.4	0	0
<i>O. laterotrema</i> (Byrd and Denton, 1938)	0	0	0	0	0	0	100	262.0 $\pm$ 37.9
<i>Dasymetra villicaeca</i> Byrd, 1935	90	97.0 $\pm$ 31.9	70	18.0 $\pm$ 6.9	73	19.0 $\pm$ 8.2	20	4.4 $\pm$ 3.7
<i>Pneumatophilus variabilis</i> (Leidy, 1856)	60	2.1 $\pm$ 0.5	17	0.5 $\pm$ 0.3	45	0.7 $\pm$ 0.3	0	0
<i>Styphlodora magna</i> Byrd and Denton, 1938	15	0.9 $\pm$ 0.4	30	1.4 $\pm$ 0.7	9	0.1 $\pm$ 0.1	80	5.2 $\pm$ 1.6
<b>Cestoda:</b>								
<i>Proteocephalus agkistrodontis</i> Harwood, 1933	0	0	0	0	0	0	80	4.0 $\pm$ 1.4
<i>P. marenzelleri</i> (Barrois, 1898)	0	0	0	0	0	0	70	2.2 $\pm$ 0.6
<i>P. perspicua</i> (LaRue, 1911)	96	16.1 $\pm$ 2.0	27	0.9 $\pm$ 0.4	55	4.4 $\pm$ 1.6	0	0
<i>P. variabilis</i> Brooks, 1978	100	156.0 $\pm$ 16.3	0	0	0	0	0	0
<b>Nematoda:</b>								
<i>Capillaria heterodontis</i> Harwood, 1932	0	0	3	0.1 $\pm$ 0.1	0	0	40	2.2 $\pm$ 1.3
<i>Cosmocercoides dukae</i> (Holl, 1928)	0	0	0	0	0	0	10	0.4 $\pm$ 0.4
<i>Falcaustra catesbeiana</i> Walton, 1929	10	0.2 $\pm$ 0.1	0	0	0	0	0	0
<i>Kalicephalus rectiphilus</i> Harwood, 1932	0	0	13	0.2 $\pm$ 0.1	0	0	30	0.5 $\pm$ 0.3
<i>Rhabdias eustreptos</i> (MacCallum, 1921)	0	0	0	0	0	0	70	2.4 $\pm$ 0.8
<i>R. fuscovenosa</i> (Railliet, 1899)	31	0.5 $\pm$ 0.1	47	2.7 $\pm$ 0.9	18	0.2 $\pm$ 0.1	0	0
<i>Strongyloides serpentis</i> Little, 1966	4	0.2 $\pm$ 0.1	0	0	0	0	0	0
<i>Terranova caballaeroi</i> Barus and Coy Otero, 1966	98	28.0 $\pm$ 2.8	97	14.3 $\pm$ 3.0	27	0.8 $\pm$ 0.5	100	22.7 $\pm$ 8.5
<b>Acanthocephala:</b>								
<i>Leptorhynchoides thecatus</i> (Linton, 1891)	27	1.3 $\pm$ 0.4	7	0.2 $\pm$ 0.2	0	0	0	0
<i>Neoechinorhynchus cylindratus</i> (Van Cleave, 1913)	15	0.3 $\pm$ 0.1	0	0	0	0	0	0

Table 3. Comparative diversity of helminth species in aquatic snakes.

	<i>Nerodia cyclopion</i>			<i>Nerodia fasciata</i>		<i>Nerodia rhombifera</i>		<i>Agkistrodon piscivorus</i>	
	Head of Island (N = 48)	Spanish Lake (N = 60)		Head of Island (N = 30)	Spanish Lake (N = 29)	Head of Island (N = 11)	Spanish Lake (N = 24)	Head of Island (N = 10)	Spanish Lake (N = 7)
Species richness	6.4 ± 0.2*	3.0 ± 0.11		3.8 ± 0.3	1.3 ± 0.2	3.0 ± 0.5	1.5 ± 0.2	6.1 ± 0.4	3.0 ± 0.8
Mean no. of individuals	321.4 ± 44.0	79.4 ± 7.3		60.9 ± 12.6	4.2 ± 1.3	34.7 ± 13.2	43.9 ± 35.9	306.1 ± 41.9	7.1 ± 2.2
Shannon-Weiner diversity (H')	0.580	0.181		0.629	0.746	0.503	0.326	0.279	0.833
Hmax'	1.079	0.954		1.000	0.903	0.845	0.845	1.041	0.954
Evenness (H'/Hmax')	0.538	0.190		0.629	0.826	0.595	0.386	0.268	0.873

\* Standard error.

Table 4. Similarities between helminth communities of aquatic snakes from Head of Island, Louisiana.

Species	<i>Nerodia cyclopion</i>	<i>N. fasciata</i>	<i>N. rhombifera</i>	<i>Agkistrodon piscivorus</i>
Jaccard's coefficient				
<i>Nerodia cyclopion</i>	—	0.57	0.58	0.16
<i>N. fasciata</i>	0.47	—	0.70	0.31
<i>N. rhombifera</i>	0.45	0.62	—	0.20
<i>Agkistrodon piscivorus</i>	0.09	0.11	0.04	—
Percent similarity				

were much higher in HOI snakes (Tables 2, 5). This trend was especially true for trematodes. For example, *D. villicaeca* infected 90% of *N. cyclopion* at HOI with a mean abundance of 97.0. At SL, this trematode infected only 8.0% of *N. cyclopion* and had an abundance value of 0.5. *Terranova caballeroi* was the most abundant nematode at HOI, but did not occur at SL. Despite these locality differences, a similar pattern of prevalence and abundance for *P. perspicua* and *P. variabilis* occurred in *N. cyclopion*. Abundance of these cestodes was significantly higher for *N. cyclopion* at HOI, but appeared to be only a difference in magnitude, as SL *N. cyclopion* were also heavily infected.

From a community perspective, both species richness and mean number of individuals were higher in HOI snakes than in SL snakes (Table 3). Species richness was significantly higher in *N. cyclopion* ( $P < 0.001$ ), *N. fasciata* ( $P < 0.001$ ), *N. rhombifera* ( $P < 0.01$ ), and *A. piscivorus* ( $P < 0.01$ ) from HOI than in conspecifics from SL. Mean number of individuals was significantly higher in *N. cyclopion* ( $P < 0.001$ ), *N. fasciata* ( $P < 0.001$ ), and *A. piscivorus* ( $P < 0.001$ ) from HOI; however, this metric was significantly higher in *N. rhombifera* ( $P < 0.05$ ) from SL. Shannon-Weiner species diversity values were higher in *N. cyclopion* and *N. rhombifera* from HOI when compared to conspecifics from SL (Table 3). Jaccard's coefficients for locality comparisons of the helminth communities of *N. cyclopion*, *N. fasciata*, *N. rhombifera*, and *A. piscivorus* were 0.62, 0.50, 0.56, and 0.43, respectively. Percent similarity values for locality comparisons of the helminth communities of *N. cyclopion*, *N. fasciata*, *N. rhombifera*, and *A. piscivorus* were 0.55, 0.51, 0.40, and 0.05, respectively. These community similarity indices indicated that the helminth community structure of *Nerodia* spp. was

**Table 5.** Prevalence and abundance (mean  $\pm$  SE) of helminths in 4 species of sympatric aquatic snakes from Spanish Lake, Louisiana.

Parasite species	<i>Nerodia cyclopion</i> N = 60		<i>N. fasciata</i> N = 29		<i>N. rhombifera</i> N = 24		<i>Agkistrodon piscivorus</i> N = 7	
	Prevalence %	Abundance	Prevalence %	Abundance	Prevalence %	Abundance	Prevalence %	Abundance
<b>Trematoda:</b>								
<i>Ochetosoma aniarum</i>	15	0.2 $\pm$ 0.1	34	0.7 $\pm$ 0.2	33	35.8 $\pm$ 33.4	14	0.1 $\pm$ 0.1
<i>O. kansense</i> (Crow, 1913)	0	0	0	0	0	0	14	1.3 $\pm$ 1.3
<i>Dasymetra villicaeca</i>	8	0.5 $\pm$ 0.3	3	1.2 $\pm$ 1.2	13	3.5 $\pm$ 2.4	0	0
<i>Pneumatophilus variabilis</i>	52	1.0 $\pm$ 0.1	17	0.2 $\pm$ 0.1	50	2.0 $\pm$ 0.7	0	0
<i>Styphlodora magna</i>	0	0	0	0	0	0	14	0.1 $\pm$ 0.1
<b>Cestoda:</b>								
<i>Proteocephalus agkistrodontis</i>	0	0	0	0	0	0	29	0.3 $\pm$ 0.2
<i>P. marenzelleri</i>	0	0	0	0	0	0	29	0.4 $\pm$ 0.3
<i>P. perspicua</i>	92	4.7 $\pm$ 0.5	24	0.4 $\pm$ 0.2	29	0.7 $\pm$ 0.3	43	0.9 $\pm$ 0.5
<i>P. variabilis</i>	95	72.1 $\pm$ 7.3	0	0	0	0	0	0
<b>Nematoda:</b>								
<i>Capillaria heterodontis</i>	0	0	0	0	8	0.9 $\pm$ 0.7	43	1.1 $\pm$ 0.6
<i>Cosmocercoides dukae</i>	0	0	3	0.03 $\pm$ 0.04	0	0	0	0
<i>Kalicephalus rectiphilus</i>	3	0.03 $\pm$ 0.02	28	1.2 $\pm$ 0.5	13	1.0 $\pm$ 0.4	71	1.7 $\pm$ 0.6
<i>Oswaldocruzia pipiens</i> Walton, 1929	0	0	3	0.03 $\pm$ 0.04	0	0	0	0
<i>Rhabdias eustreptos</i>	0	0	0	0	0	0	14	0.4 $\pm$ 0.4
<i>R. fuscovenosa</i>	12	0.6 $\pm$ 0.4	21	0.5 $\pm$ 0.2	8	0.1 $\pm$ 0.1	0	0
<i>Strongyloides serpentis</i>	2	0.03 $\pm$ 0.03	0	0	0	0	0	0
<b>Acanthocephala:</b>								
<i>Neoechinorhynchus cylindratius</i>	15	0.3 $\pm$ 0.1	0	0	0	0	0	0

**Table 6.** Similarities between helminth communities of aquatic snakes from Spanish Lake, Louisiana.

Species	<u>Nerodia cyclopion</u>	<u>N. fasciata</u>	<u>N. rhombifera</u>	<u>Agkistrodon piscivorus</u>
	Jaccard's Coefficient			
<u>Nerodia cyclopion</u>		0.55	0.60	0.20
<u>N. fasciata</u>	0.09		0.67	0.21
<u>N. rhombifera</u>	0.04	0.33		0.33
<u>Agkistrodon piscivorus</u>	0.06	0.39	0.08	
	Percent Similarity			

most similar between localities and that helminth community structure of *A. piscivorus* was least similar between localities.

### Discussion

Based on patterns in the helminth communities of birds, fishes, and a mammal, Kennedy et al. (1986) predicted that host physiology, host vagility, breadth, and selectivity of diet, complexity of the alimentary canal, and host exposure to helminths with direct life cycles were important factors that contributed to helminth community structure and diversity. Results of the present study indicate that several of these factors also had great predictive value for comparison of aquatic snake helminth communities. Dietary differences, both among species of water snakes and between water snakes and cottonmouths, have been well documented (Mushinsky, 1987). Furthermore, those species of snakes that include a large proportion of tadpoles in their diet would be expected to harbor a rich trematode fauna, as tadpoles are commonly utilized as second intermediate hosts for most snake trematodes. At HOI, the high abundance of trematodes in *N. fasciata* may be a reflection of the diet of this snake, which includes many anurans (Mushinsky et al., 1982). Similarly, high helminth species diversity and evenness occurred in *N. fasciata* at HOI and SL, and this may be attributed to the euryphagic nature and generalized habitat preference of this snake (Mushinsky and Hebrard, 1977; Hebrard and Mushinsky, 1978). Conversely, prior to our study we expected that *N. cyclopion* would have a relatively depauperate helminth fauna since this snake has been reported to be piscivorous

throughout its life (Mushinsky et al., 1982). This pattern existed at SL, but conspecifics from HOI harbored helminths with much higher prevalence and abundance. One explanation for this difference is that *N. cyclopion* may have a broader diet than previously suggested and population differences in foraging ecology could be a factor contributing to the different helminth fauna between the 2 localities. While *Gambusia affinis* and centrarchid fish were common food items recovered from *N. cyclopion* at both HOI and SL, tadpoles (*Rana* sp.) were only found in snakes from HOI. Furthermore, Garton et al. (1970) reported salamanders (*Siren intermedia*) and centrarchids in stomachs of *N. cyclopion* from Illinois.

In our study, those host species with low sample sizes might have affected our overall conclusions concerning helminth occurrence. However, based on the high prevalence and abundance of many helminths, particularly in HOI snakes, our sampling would likely have included most of the helminths that parasitize aquatic snakes. Low helminth species diversity and evenness in *A. piscivorus* from HOI is likely due to a single species, *O. laterotrema*, which dominated the community of this snake. At SL, comparisons among snake species were more difficult due to poor colonization by helminths. For example, 3 species of trematodes were most abundant in *N. rhombifera*, while at HOI, these same species were more abundant in *N. cyclopion* and *N. fasciata*. Additionally, *S. magna* was only found in *A. piscivorus* at SL, but infected all species of snakes at HOI. Highest species richness and mean number of individuals in *N. cyclopion* and *A. piscivorus* is primarily due to the high prevalence and abundance of cestodes in these snakes.



Helminth community structure of HOI snakes was richer and more diverse than conspecifics from SL. One apparent locality difference that may be explained is the higher trematode abundance that occurred in HOI snakes as compared with that in SL snakes. A common factor shared by the trematodes reported in this study is the utilization of physid snails as first intermediate hosts. While snail abundance was not measured at our study sites, helminth survey data indicate that trematode transmission at SL was not as successful as at HOI, which might be a reflection of low snail densities. Qualitatively, habitat perturbation and environmental variability at SL was greater than at HOI. During this study, spoil bank construction and other anthropogenic disturbances were common at SL. However, the most influential factor was likely the extreme fluctuations of water level observed at SL. Furthermore, the SL locality differed from HOI in having greater expanses of open water, whereas the HOI locality consisted of a major waterway, the Petite Amite river, which was closely surrounded by swamp. For cestodes, which are not dependent on a snail intermediate host, abundance was more similar between localities. Nematodes of the genus *Rhabdias* were similar in abundance between localities and this possibly is due to their direct life cycle pattern. Further, *Kalicephalus rectiphilus* was actually more abundant in SL snakes than in HOI snakes. However, *Terranova caballeroi* was very abundant in HOI snakes, but absent from SL. Locality differences found in our study appear to be correlated with the life history strategy of particular helminth taxa and are very important in determination of helminth community organization of aquatic snakes. For example, if our study had only considered SL, then we would have concluded that aquatic snakes harbor a relatively depauperate helminth fauna.

Based on comparisons of our study with the data of Collins (1969) and Dettlerline et al. (1984), it appears that the trematode genera *Dasymetra*, *Ochetosoma*, *Pneumatophilus*, and *Styphlodora* characterize the helminth community of aquatic snakes. Taxonomic questions and uncertainties exist at the species level of these trematode genera, precluding a more specific analysis. Qualitatively, it appears that, regardless of locality, aquatic snakes host a similar suite of helminth parasites that are not shared with other reptiles or amphibians. However, it should be noted that quantitative differences in the helminth fauna (as

reported in the present study) may be locality-dependent. A total of 19 helminth species at HOI and 17 species at SL were recovered in the present study. Dettlerline et al. (1984) included snakes collected from discrete populations in Perry County, Alabama. They recovered only 10 species of helminths, including 2 species of pentastomids, from *Agkistrodon piscivorus*, *Nerodia erythrogaster*, *N. rhombifera*, and *N. sipedon*. Prevalence of *Ochetosoma aniarum* (90%) in *N. erythrogaster* and of *Proteocephalus perspicua* (58%) in *N. rhombifera* were reported by Dettlerline et al. (1984) and are comparable to our findings. Helminth community structure of snakes in the Alabama survey was similar to the present study in that the helminth fauna of *Nerodia* spp. was most similar, while *A. piscivorus* shared only 1 helminth species (*P. perspicua*) with water snakes. Collins (1969) reported 18 species of helminths, excluding larval forms, from *N. sipedon*, *N. erythrogaster*, and *N. taxispilota*, and 10 species of helminths from *A. piscivorus* from 8 counties in eastern North Carolina. Trematodes also were prevalent in his study with >80% prevalence of *O. aniarum* in *N. sipedon* and *N. erythrogaster*. Prevalence of 81% for the cestode *P. marenzelleri* in the North Carolina survey was similar to the prevalence (70%) recorded in *A. piscivorus* from HOI. In addition, Collins found that a nematode, *Terranova* sp., was very prevalent (>80%) in *N. erythrogaster*. In our study, prevalence of >97% was recorded for *Terranova caballeroi* in *N. cyclopion*, *N. fasciata*, and *A. piscivorus* at HOI. The occurrence of this nematode in piscivorous snakes suggests that a fish host may be involved in the life cycle since another related species, *T. crocodili*, is known to utilize fish (*Lates calcarifer*) as an intermediate host (Sprent, 1979). Abundance of *T. caballeroi* was lower in *N. rhombifera*, a snake that preys on different species of fish (catfish, shad), than in *N. cyclopion* and *N. fasciata*, which eat mainly mosquitofish and centrarchids (Mushinsky and Hebrard, 1977). Collins (1969) also reported that the helminth fauna of *A. piscivorus* was distinct when compared to *Nerodia* spp., with four helminths restricted to cottonmouths. In his study of snake trematodes, Rabalais (1967, 1969b) examined 11 genera and 14 species of snakes from various parishes in Louisiana. The host distribution of trematodes in the present study was in agreement with the data of Rabalais (1967, 1969b), and no new host records were found.

Broad overlap in diet and habitat preference



of *Nerodia* spp. and their close phylogenetic affinities are probably the proximate causes of the similarity of their helminth fauna. Aho (1990) suggested that host specificity was unimportant for the helminths of amphibians and reptiles. In our study, host generalists were found (e.g., *Styphlodora magna* and *T. caballeroi*), but many host specialists existed in the helminth fauna of *A. piscivorus*. *Ochetosoma laterotrema*, *O. kansense*, *P. agkistrodontis*, *P. marenzelleri*, and *R. eustreptos* were all specific to *A. piscivorus*. Rabalais (1967, 1969b) also found that *O. kansense* and *O. laterotrema* occurred only in *A. piscivorus*. Our data, from both localities, indicate that *Nerodia* spp. harbor different species of *Ochetosoma*, *Proteocephalus*, and *Rhabdias* than cottonmouths. Support for this apparent phylogenetic component exists in that *A. piscivorus* is known to prey on many of the same food items as *Nerodia* spp. (Kofron, 1978). Furthermore, *O. laterotrema* has been experimentally demonstrated to be specific to cottonmouths (Sogandares-Bernal and Grenier, 1971). The specificity of *P. variabilis* for *N. cyclopion* is unknown. Brooks (1978) described *P. variabilis* and listed both *N. cyclopion* and *N. rhombifera* as hosts. Because *N. cyclopion* is piscivorous, it is interesting that *P. variabilis* is abundant in this host. Snake cestodes (*Proteocephalus*) have a life cycle that utilizes tadpoles as a second intermediate host (Thomas, 1941); therefore, infection of piscivorous snakes may indicate that fish also serve as intermediate hosts.

Because helminth prevalence and species richness of all snakes was not found to differ significantly with regard to host sex, it appears that males and females are equally exposed to helminth infections. However, mean number of individuals and abundance data for *O. aniarum* and *D. villicaeca* indicated that females of *N. cyclopion* were more heavily parasitized than males. We cannot explain this sexual difference, but dietary differences between males and females could account for this pattern.

Data concerning age of wild-caught snakes are not currently available. Therefore, our analysis of helminth infections in snakes is based on the assumption that body size is a reasonable indicator of age. For the purposes of our study, snakes that are less than 1 year old would probably not be exposed to as many helminths as would snakes that have completed their first full year of life. By comparing the body sizes of aquatic snakes recorded in the present study with neonate body

sizes of conspecifics (Dundee and Rossman, 1989), it was determined that most snakes examined during this study would likely be at least 1 year of age. One exception was a specimen of *N. rhombifera* from SL, which was of a size comparable to a young-of-the-year snake.

Several helminths that were recovered in our study appear to be accidental parasites of snakes. *Cosmocercoides dukae*, *Falcaustra catesbeiana*, and *Oswaldocruzia pipiens* usually infect amphibians and *Leptorhynchoides thecatus* and *Neoechinorhynchus cylindratus* normally infect fish hosts. The occurrence of these helminths may be explained by the inclusion of frogs and fish in the diet of aquatic snakes. Anderson (1935) also reported that *L. thecatus* was prevalent (21%) in *N. sipedon* from Ohio and considered the infection accidental, noting that the acanthocephalan was probably acquired by snakes eating infected fish.

Several factors that may play important roles in structuring the helminth community of aquatic snakes include the ecology of the host, phylogeny of the host, local environmental conditions, and other ecological factors such as seasonal changes in helminth populations. Our contribution is that we have addressed the first of these factors, host diet, host phylogeny, and effects of locality differences on snake helminth communities, providing a foundation on which other factors such as habitat differences and seasonal changes can be based.

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